Assessment of potential for remote sensing detection of bark beetle-infested areas during green attack: a literature review

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Abstract

Changes observed in the foliage of trees killed by bark beetles are usually described in terms of stages that have been related to a specific timeframe. The "green attack" stage is the period of time, typically one year long, in which the needles of newly colonized trees remain essentially green before turning gradually red.

A review of the existing literature is presented in this report as an attempt, based on existing knowledge, to evaluate the possibility of detecting, with remote sensing, infested areas of forests in the "green attack" stage of infestation. The emphasis is on the expected biophysical changes of the trees and their foliage. Other important aspects, such as sensor characteristics and observation strategies, have not been considered here.

The process of tree colonization by the bark beetle is presented to highlight the most important aspects of the insect–host interaction. The controversy about the role of the fungi in killing the tree is then reviewed. Attacked trees will likely experience a progressively severe water stress caused by xylem disruption. The expected response of a plant under moisture deficit and the possibility that the tree may offset the symptoms is discussed.

Finally, a brief review of works on remote sensing detection of vegetation water content, vegetation stress, and foliar nitrogen is presented to demonstrate the capability of this technique to retrieve information on bark beetle outbreaks.

Key Words: *Dendroctonus ponderosae*; mountain pine beetle; *Pinus contorta*; lodgepole pine; green attack, remote sensing, detection, bluestain fungi, vegetation water content, vegetation stress, foliar nitrogen

Résumé

Les changements constatés dans le feuillage des arbres dévastés par les scolytes sont généralement décrits en fonction des stades associés à des périodes précises. Le « stade vert » correspond à la période, généralement d'un an, durant laquelle les aiguilles des arbres nouvellement colonisés demeurent essentiellement vertes avant de tourner progressivement au rouge.

Dans le présent rapport, les documents existants sur le sujet sont passés en revue dans le but d'évaluer la possibilité de déceler, par télédétection, les secteurs forestiers infestés se trouvant au stade vert de l'infestation. L'accent est mis sur les changements biophysiques attendus dans les arbres et leur feuillage. D'autres facteurs importants, tels que les caractéristiques des capteurs et les stratégies d'observation, ne sont pas pris en compte dans le présent document.

On décrit le processus de colonisation des arbres par les scolytes en vue de mettre en évidence les aspects les plus importants de l'interaction insecte-hôte. La controverse au sujet du rôle des champignons dans la mort des arbres est ensuite examinée. Les arbres attaqués subissent probablement un stress hydrique de plus en plus grave occasionné par la perturbation du xylème. On examine aussi la réaction attendue d'une plante souffrant d'un déficit hydrique et la possibilité que l'arbre puisse neutraliser les symptômes.

Enfin, on présente un examen sommaire des travaux de télédétection de la teneur en eau de la végétation, du stress de la végétation et de l'azote foliaire afin de faire le point sur la capacité de cette technique de fournir des informations sur les infestations de scolytes.

Mots clés: *Dendroctonus ponderosae*; dendroctone du pin ponderosa; *Pinus contorta*; pin tordu latifolié; stade vert d'infestation, télédétection, détection, champignons agents du bleuissement, teneur en eau de la végétation, stress de la végétation, azote foliaire

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Introduction

Primary bark beetles of the family *Scolitidae* are known to cause extensive mortality in conifer forests as a result of periodic outbreaks. The loss of large forested areas is of ecological and economic concern. The close monitoring and mapping of beetle population dynamics is the first step towards the development of any strategy aiming to control the spread of these insect species. Monitoring of forest ecosystems through digital remote sensing techniques has greatly improved in recent years, and the technology now available seems suitable for routine use in many forest management applications (Wulder 1998; Treitz and Howarth 1999; Lefski et al. 2001; Wang et al. 2004).

Bark beetle outbreaks potentially can be mapped using remote sensing instruments that read induced physiological and visual effects of the attack in forest canopies. Three stages are recognized to affect the foliage of trees successfully attacked by primary bark beetles. The green attack stage occurs during host colonization and early establishment by the beetle population, when no apparent visual symptoms are detectable at the canopy level. Initially during this phase, an attacked tree is still physiologically alive although stressed beyond recovery, with death being an eventuality. More importantly, the newly hatched generation of beetle is developing within the inner bark at this time. The red attack and gray attack stages usually develop within one and three years, respectively, from the moment of first mass attack. During these stages, the tree canopy first gradually turns red-brown (hence the name red attack); then, progressive defoliation follows (gray attack). Some overlap is usually observed between the development of red attack and the onset of gray attack. All trees in these two stages are dead and have been abandoned by the new beetle generation.

Remote sensing detection of red and gray attacks has been attempted, with mixed results, for the past three decades, using mostly aerial photography and visual interpretation. More recently, change detection techniques (Collins and Woodcock 1996) and tasseled cap transformation applied to Landsat imagery (Price and Jakubauskas 1998; Skakun et al. 2003) have shown positive results in monitoring forest disturbance and mortality as a result of insect infestation. A study by Franklin et al. (2003) is relevant because it is based on an automatic detection algorithm for red attack damages instead of being based on visual interpretation.

For scientific and forest management purposes, however, the most important phase to be monitored is the green attack stage. It has proven to be much more difficult and elusive to detect by remote sensing techniques because of the lack of apparent visual symptoms. Carter et al., (1998) used airborne imagery acquired at 1-m spatial resolution in three narrow spectral bands centred at 675, 698, and 840 nm to detect southern pine beetle (*Dendroctonus frontalis* Zimm.) damage in a mixed conifer and hardwood forest of the Ouachita National Forest, Arkansas. Heavily damaged trees with chlorotic foliage were easily identified by means of a normalized difference vegetation index (NDVI), but trees in the green attack stage were not easily resolved visually from healthy trees, based on the same type of information. It seems that the natural variation in chlorophyll content among healthy trees was sufficient to mask most of the change in pigmentation in damaged trees. More recently, Heath (2001) used Compact Airborne Spectrographic Imager (CASI) imagery to investigate green attack damages caused by mountain pine beetle (*Dendroctonus ponderosae* Hopk.) in a forested area near Williams Lake, British Columbia. Data collected in 36 spectral bands between 427 nm and 977 nm at the spatial resolution of 0.6 m were used in this study. Discrimination of recently damaged trees from healthy ones was problematic in this case, although four narrow spectral bands centered at 539.5 nm, 645.4 nm, 706.4 nm, and 829.4 nm emerged as promising for differentiating damaged trees from healthy trees. To confirm the validity of these bands, further investigations were suggested.

Interactions among bark beetles, associated fungi, and host trees

In order to better understand and assess the possibility of detecting trees in the green attack stage by remote sensing, it is essential to examine in detail the interrelations between the beetle and host tree in this early phase of mass attack.

Paine et al. (1997) and Raffa (2001) summarize the basic functions of bark beetles as:

1. selection, colonization, and exploitation of host trees,
2. mating,
3. competition avoidance, and
4. predation avoidance.

It is not well understood how bark beetles species select suitable host trees. Semiochemical cues embedded within the complex mix of terpenes released by the trees play a central role because the beetles are able to discriminate suitable compound combinations, perhaps detecting differences in their ratio (Pureswaran et al. 2004).

In addition, tree stress and vigor are important factors when a beetle population is at the endemic level. For instance, Smith et al. (2002) found that lodgepole pine trees characterized by a Waring vigor index (WVI) lower than 100 g of stemwood production per m^2 on an Oregon site were more intensely attacked by mountain pine beetle than trees above this threshold. Although the threshold value of 100 g/m^2 cannot be generalized, it suggests that tree physiological conditions are important in host selection by primary bark beetle species. At the epidemic level, however, the beetles also attack trees of high vigor (Paine et al. 2997).

After pioneer attacks are successfully completed, the beetles use aggregating pheromones to generate mass attacks by a high number of conspecifics on selected host trees, and favor their colonization (Raffa 2001; Pureswaran et al. 2004; Bentz et al. 1997). A threshold, represented by the number of attacks per bark unit area, must be reached to overcome tree resistance while, at the same time, avoiding excessive competition for the limited resources represented by the tree's inner bark. According to Paine et al. (1997), mass attack usually peaks within two to three days following first attack, and the attack itself is terminated in just over five days. Oviposition starts only after tree resistance is overcome. The microhabitat of primary bark beetles is within the tree phloem. The insects have a life cycle of one year, and leave the tree only to find a new host to start the new generation of beetles.

A variety of fungi species (for example, *Ophiostoma* and *Ceratocystis* spp.), capable of infecting both phloem and sapwood, is usually found in symbiosis with bark beetles (Paine et al. 1997; Six et al. 2003). The interrelation of beetle–fungi–host tree is complex and not well understood. The relation between beetle and fungi is considered mutualistic, as the fungi use the beetles as vectors to access and infect new trees, while the beetles likely benefit from the fungi in a variety of ways: some fungi species are a direct source of food for the new insect larvae; other fungi species can also affect the nutritional quality of the phloem, making it more palatable to the beetles. Almost certainly the fungi have a critical role in helping the beetles in killing the host trees. At the same time, fungi may compete with beetles in exploiting the tree's limited resources. Competition also occurs among fungus species with different degrees of pathogenicity that find their way within the phloem and sapwood (Paine et al. 1997; Klepzig et al. 2001; Klepzig and Wilkens 1997).

Although it has been observed that a large amount of staining fungi can significantly alter water retention within a tree and even cause its death, it is uncertain whether the beetles or the fungi are primarily responsible for tree mortality. The beetles' phloem-colonization phase and the fungi's sapwood-

colonization phase occur at very different times. Subsequent phloem exploitation by the beetle and developing new larvae and pupae may be comparable in terms of time length, and this can have implications for the physiology of the attacked trees and for detection of green attack by means of remote sensing.

The beetle–fungi association essentially attacks and impairs the tree vascular system that is composed of secondary xylem and phloem that forms at the vascular cambium. Water that is loaded with nutrients (sap) moves up into the xylem (sapwood) along the soil–plant–air–continuum pathway. In conifers, the sap is driven by pressure gradients within the vertically overlapping xylem tracheids organized in series of adjacent rows. Tracheids are interconnected by means of small, specialized pits located in tracheid walls. Mature tracheids are no longer composed of living tissue, even though they may still transport water (Kozlowski and Pallardy 1997; Taiz and Zeiger 2002). In conifers, ascending sap often follows a spiral pathway (Kubler 1991). Sap velocity in relation to sapwood thickness has been measured by Phillips et al. (1996) in *Pinus taeda* saplings, and by Wullschleger and King (2000) in yellow-poplar (*Liriodendron tulipifera* L.): sap velocity clearly decreased with sapwood thickness. Wullschleger and King (2000) also estimated the fraction of sapwood functional in water transport as being in the range of 0.49 to 0.96 (average = 0.66). The sapwood that is active in the transport of water and nutrients is less than the total sapwood available. This is particularly important when considering potential disruption to water transport in a tree by staining fungi. Recent measures of sap flux density in *Pinus* spp. confirm observed distribution patterns of previous experiments, with a higher sap flux density occurring near the cambium and progressively decreasing values occurring toward the inner core of the stem. The detected radial profiles, however, varied from tree to tree, and within trees, in relation to time of day. Late in the day, the shape of the sap flux density tends to flatten by increasing the proportion of sap flux from the inner part of the xylem (Ford et al. 2004).

The phloem is primarily responsible for the translocation of the photosynthate from its areas of production, mostly in the leaves, to plant sinks, and is primarily formed by sieve cells. Contrary to the mature tracheids of the xylem, the phloem is composed of living tissue (Koslowski and Pallardy 1997; Taiz and Zeiger 2002).

The vascular system as a whole also has an important role in the transportation of hormones and other information molecules that are used to signal stress conditions and trigger defense responses by the plant (Ruiz-Medrano et al. 2001). Signaling pathways form a complex network characterized by both crosstalk and specificity aspects. Nonetheless, the complexity of the signaling network is mirrored by equal complexity of plant-stress responses (Shinozaki and Yamaguchi-Shinozaki 1997). Phloem disruption and mortality result from the girdling action of the beetles and, possibly, from the pathogenicity of some fungus species. Consequently, translocation of photosynthate is also interrupted or greatly impaired in many areas along the tree stem.

Sapwood occlusion is often attributed to the gradual penetration of hyphae into the xylem, as well as to possible plugging of tracheids by tree resin. Aspiration of the tracheid pits tori, direct plugging of the pits by hyphae or by particles released by the fungi, and induction of xylem cavitation are likely mechanisms by which staining and, perhaps, non-staining fungi disrupt water uptake and contribute to the death of the tree. An increase in transpiration rate, induced by some isocumerin toxins produced by fungi, is also a candidate in determining progressively increasing effects of water stress in attacked trees (Paine et al. 1997; Nebeker et al. 1993); nonetheless, Croisé et al. (2001) have pointed out that, despite massive fungal infection that may be correlated with xylem disruption, relatively few quantitative analyses of fungal effects on hydraulic conductivity have been reported in the literature. Moreover, some of those that are reported challenge the hypothesis that the fungi are primarily responsible for tree mortality in beetle mass

attack. Parmeter et al. (1992) inoculated two stands of *Pinus ponderosa* (a total of 98 trees) with *Ophiostoma minus* and *Leptographium terebrantis*. Inoculations between the two stands took place two years apart. Mean length of lesions, depth of sapwood occlusion, and proportion of sapwood occlusion were measured weekly for the first six weeks, then after 9, 17, and 64 (62 in one stand) weeks following inoculation. All three parameters increased for the first 4 to 5 weeks, after which the values became erratic, particularly for length of lesion and depth of sapwood occlusion. The mean proportion of sapwood occlusion did not exceed 0.3 for *Ophiostoma minus* at any time during the measurement period. Infections of *Leptographium terebrantis*, a more virulent fungus, produced higher values of proportion of sapwood occlusion, but values exceeded 0.5 to 0.7 only after 17 weeks. A peak of 0.92 sapwood occlusion was measured only after 62 weeks, but this high value may have been affected by the small average diameter of sampled trees. The low occlusion values for *Ophiostoma minus* and the length of time required by *Leptographium terebrantis* to develop substantial sapwood occlusion were inconsistent with visible crown-wilting symptoms and tree death reported for some beetle–fungi attacks on ponderosa pines. The authors estimated that a 2:3 ratio of sapwood occlusion within a period of 1 to 4 weeks may be compatible with rapid tree decline and death. Solheim (1995) also reported low values of sapwood occlusion depth in *Pinus contorta* after two weeks following colonization by mountain pine beetle (*Dendroctonus ponderosae*). Ross and Solheim (1997) artificially inoculated 48 Douglas-fir (*Pseudotsuga menziesii*) trees on the Siuslav National Forest, Oregon, using three different doses of *Ophiostoma pseudotsugae* and *Leptographium abietinum* applied in 60-cm-tall bands around the trees' circumferences. Some of the trees were also pruned by about 30% to determine if pruning affects tree resistance. After five months the trees were felled and examined in detail. Mean percentage values of sapwood occlusion were 38.7% for *Ophiostoma pseudotsugae* and 30.2% for *Leptographium abietinum*, although the difference was not statistically significant. None of the trees were dead before felling, although some were chlorotic. The percentage of functional sapwood for the chlorotic trees was less than 30%. The authors concluded that these fungi likely assist bark beetles in killing host trees, although the presence of some chlorotic trees does not rule out the hypothesis that these fungi may directly kill a tree under specific conditions and within appropriate lengths of time.

Because of reports that drought may enhance the likelihood of trees being attacked by bark beetles, Croisé et al. (2001) conducted an experiment on 48 potted 5-year-old Scots pines (*Pinus sylvestris* L.). The trees were divided into three groups, and four treatments were applied to different trees in each group: 1) drought cycles and inoculation with *Leptographium wingfieldii*; 2) drought cycles only; 3) watered trees and inoculation with *Leptographium wingfieldii*; 4) watered trees only. The experiment lasted six months. Watered trees suffered only minor lesions 2.5 months after inoculation; drought-stressed and inoculated trees suffered visible damage to sapwood as well as loss of specific conductivity of between 50% and almost 100% in some samples. Trees subjected to drought cycles only showed symptoms of xylem cavitation with a decrease of hydraulic conductivity, but no visible damage to sapwood. Drought also caused a decrease in the growth rate of stem diameter. The experiment demonstrated that moderate to severe drought enhances the susceptibility of Scots pines to beetle–fungi attack.

Host trees are not passive victims of bark beetle attacks. Conifer trees react with constitutive (preformed) and induced (hypersensitive) responses (Nebeker et al. 1993). Pine and spruce species have an elaborate network of resin ducts through which a conspicuous amount of preformed and stored oleoresin is allowed to flow to mechanically wounded areas. Oleoresin secretion represents the first and most important attempt by the tree to react to initial beetle attack (Baier et al. 2002). Oleoresin is a complex mixture of terpenoids and resin acids with toxic and antibiotic properties. Its secretion toward a wounded area is meant to accomplish a dual function: to flush the wound, and to seal or isolate it from adjacent

intact tissues. Preformed oleoresin is secreted to pitch out beetles and associated fungi, while the sealing of the injured tissue stops the spread of parasites and fungi within the wood (Paine et al. 1997; Trapp and Croteau 2001). The composition and, above all, the amount of preformed oleoresin depend on plant physiological status, season, and environmental conditions (Lombardero et al. 2000). *Abies* and *Tsuga* species lack the elaborated resin duct network and storage of preformed oleoresin that characterize pine and spruce species. When attacked by bark beetle, *Abies* and *Tsuga* rely on the production and secretion of secondary resin for defense. This form of induced response is more localized, and the amount of secreted resin is usually less than that of the constitutive response. The resin also has a slightly different chemical composition than the preformed resin (Paine et al. 1997; Nebeker et al. 1993). Environmental conditions and tree vigor affect the production of secondary resin as well.

Besides secretion of resin, other forms of induced response involve cellular and biochemical changes. Cellular necrosis around injured tissue and concentration of tannin and phenolic compounds in the phloem are typical induced responses. Paine et al. (1997) and Nebeker et al. (1993) point out that it is usually possible to observe enormous variation in intensity of induced responses, both within a tree and between trees. Successful mass attacks by beetles are able to drain constitutive reserves of oleoresin within about six days. A strong decrease, or cessation, in resin flow is a sign that host defenses have been overcome and the tree will not be able to recover (Paine et al. 1997). At this point, sapwood staining and occlusion is also likely to progress because of the proliferation of beetle-associated fungus species. The onset and development of moisture stress is then the most probable outcome of sapwood occlusion by fungi proliferation.

Tree water stress

No biophysical and biochemical aspect of plant functioning is unaffected by moisture deficit; however, the chain of events that takes place in dying trees is difficult to predict. As already mentioned, the length of time required for moisture deficit to produce visible symptoms in foliage can vary from weeks to several months. Tree anatomical and physiological characteristics explain differences in behavioural responses due to moisture deficit. For instance, Stout and Sala (2003) found that shoots and roots of ponderosa pine are more vulnerable to water stress-induced cavitation than shoots and roots of Douglas-fir are. However, ponderosa pine has a large proportion of sapwood that can store water, giving the species the ability to thrive in drier environments better than Douglas-fir does. In addition, ponderosa pine has a higher stomatal sensitivity, allowing for greater control of transpiration rates. It is reasonable to expect, therefore, that ponderosa pines in green stage attack may offset negative effects of moisture deficit, perhaps for several weeks. According to Stout and Sala, Scots pines have the same capability to store water in the xylem as a reserve for periods of drought.

Thus, it is possible that responses to the onset and intensification of water stress during the early phase of green attack will vary from species to species and from tree to tree within a species as a function of stress level, tree age, and location. However, considering beetle mass attacks are carried out mainly in July and August, there is little chance that severe moisture deficit will affect attacked trees before the subsequent winter season. In addition, conifer needles are particularly well equipped to respond quickly to moisture deficit. They have evolved to deal with dry environments and to minimize water loss. Anatomical characteristics of conifer needles related to moisture content include sunken stomata that are protected by overarching subsidiary cells, thick epidermal cells, and cuticles of various thickness (Kozlowski and Pallardy 1997; Gifford and Foster 1989). During water stress, one of the first reactions at the leaf level is stomatal closure. This is a common, well-known physiological response that the stressed plant adopts to minimize further water loss and cell dehydration. With persistent water-stress conditions,

stomatal closure will temporarily offset xylem cavitation and damage to the photosynthetic apparatus (Taiz and Zeiger 2002; Larcher 2003; Chaves et al. 2003).

What triggers stomatal closure in desiccation conditions is not clear and a source of controversy (Brodribb and Holbrook 2003). It is difficult to understand stomatal behaviour because at any time it is also affected by CO_2 concentration and light intensity (Chaves et al. 2003). Chemical signals—in particular Abscisic Acid (ABA), which is a hormone directly involved in plant water stress—and hydraulic signals are possible candidates. Parks et al. (2002) have examined the production and delivery of ABA in mature Scots pines during an 11-month gradually imposed drought. ABA was effectively detected in the xylem sap of sampled trees, increasing its level in response to increased drought. Based on measures of sap velocity, however, the authors calculated that in conditions of severe drought, an ABA-mediated signal produced in the roots would take 6 weeks to reach the needles, traveling along a 15-metre-tall stem. This implies that a more direct control of stomatal closure is involved, and there is increasing evidence that changes in xylem conductance could send a rapid hydraulic signal to trigger stomatal closure (Chaves et al. 2003; Brodribb and Holbrook 2003; Jackson et al. 2000). Acting as a pressure regulator, stomatal closure is meant to preserve hydraulic continuity and to limit occurrence of xylem cavitation (Borghetti et al. 1998; Sperry et al. 2002).

A hydraulic control of stomatal closure seems consistent with the initially light moisture-stress conditions caused by progressive sapwood occlusion by staining fungi. If attacked trees are able to respond quickly to the first symptoms of sapwood occlusion by limiting water loss and improving water-use efficiency, detectable changes in leaf reflectance during this early stage of green attack may be offset for a period of time, or be so minimal as to remain within the natural range of variation that is typical of healthy trees.

Changes in foliar chlorophyll content naturally occur in conifers during the fall and winter seasons as a result of dormancy and frost hardening. Photosynthetic acclimation is required in order to protect foliage against photo-oxidative damages. Combined mechanisms involved in photosynthetic acclimation are the reduction of antennae size, a partial loss of photosystem II, and dissipation of absorbed light as heat through a sustained non-photochemical quenching. Non-photochemical quenching is carried on by de-epoxidation of the xanthophyll-cycle pigments, along with the protonation of chlorophyll-binding proteins. The mechanisms are reversed during spring, with a full recovery of photosynthetic capacity by the needles (Öquist and Huner 2003).

It is not known if and how recovery of photosynthetic capacity proceeds in attacked trees. The spring subsequent to the period of mass attack could represent an early opportunity to detect, using remote sensing instrumentation, changes in foliar optical properties related to green attack.

Remote sensing detection of vegetation water content, plant stress, and vegetation nutrients

The most apparent symptoms on foliar optical properties should be related to water stress. The most general response of dehydrating leaves is an increase in reflectance throughout the visible and the middle-infrared. The spectral range, 1300 to 2500 nm, is affected by the greatest changes (Aldakheel and Danson 1997).

Remote sensing determination of vegetation water content in the optical middle-infrared domain derives from extensive laboratory and field research. Leaf reflectance and leaf water content have been linked to defining spectral indices and through regression analysis. More recently, a number of leaf radiative transfer models have been created and improved, providing opportunity to further investigate the capability of detecting vegetation water content. The process of scaling-up these results at the canopy level have been only partially successful. Ustin et al. (1998) were able to predict water content of chaparral vegetation using AVIRIS data, a modified version of the PROSPECT model, and an analytical technique known as Hierarchical Foreground/Background Analysis (HFBA). The study demonstrated how remote sensing can detect, with reasonable accuracy, vegetation water content at the leaf, canopy, and landscape levels.

Serrano et al. (2000) tested the ability of the Water Index (WI; R900/R970) and the Normalized Difference Water Index (NDWI; R860 – R1240/R860 + R1240) to determine the relative water content of chaparral vegetation from AVIRIS imagery. Both indices were found effective in detecting differences in vegetation water status, although a dependence from canopy structure was noted.

Model inversion methods are constantly refined to extract information about canopy water content. Recently, Zarco-Tejada et al. (2003) performed a modeling study to verify the possibility of retrieving leaf equivalent water thickness from MODIS reflectance data of vegetation canopy and radiative transfer model inversion. The already mentioned NDWI and the Simple Ratio Water Index (SWRI; R860/R1240) were chosen to determine vegetation water content.

A study by Ceccato et al. (2001) indicated that SWIR (shortwave infrared) and NIR (near infrared) reflectance bands both are necessary to estimate leaf equivalent water thickness using remote sensing methods. This is consistent with the results of a study by Sims and Gamon (2003), in which the 1150 to 1260 nm and 1520 to 1540 nm spectral regions have been found useful for retrieving vegetation water content from satellite remote sensing.

The unifying characteristic of the work presented in this overview on vegetation water content determination by remote sensing is the direct measurement of water content. Alternative methods have also been developed and applied. Of relevance in this context are those studies that are based on links drawn between chlorophyll and water contents, and between vegetation stress and water content. Although potentially useful, the former methods are based on the assumption that chlorophyll and water contents are directly related to each other. The assumption is not always correct and should be verified case by case. Causes of chlorophyll variation can be natural (e.g., phenological status and radiation stress) or anthropomorphic (e.g., atmospheric pollution and toxic substances). Also, the relation between vegetation stress and water content is not unequivocal. Carter (1993) investigated the changes in leaf reflectance in relation to a variety of stressors in the 400 to 2500 nm range. For vegetation under stress, the observed general behaviour was a consistent increase of leaf-reflectance values in the visible range and often also in the infrared. No unique matches between any given stressor and visible reflectance were found, although a limited level of discrimination was possible.

Carter and Knapp (2001) focused their investigation on the visible range, with particular emphasis on leaf optical properties near 700 nm. A number of different stressors were considered in this case. Among samples studied, the optical properties of needles of mature loblolly pine recently attacked by southern pine beetle were compared to those of needles of healthy trees. All needles were collected from green trees. A modest increase in the visible wavelengths was observed, and the wavelength at which the needle samples differed most was 716 nm. Links to chlorophyll concentration for all type of stressors were also drawn. A concluding remark by the authors was that leaf-reflectance responses to stress are too generic to uniquely identify specific stressors.

Water deficit implies a reduction in mineral-nutrient uptake by the plant. A study by Eckstein et al. (1999) determined that evergreens have a typical leaf life span of between 1.3 and 17 years. Conifer species have the highest values. There are noticeable differences in nutrient conservation and resorption between deciduous and evergreen leaves. For instance, woody evergreens have the longest residence time for nitrogen, but mature evergreen leaves have lower nutrient concentrations than deciduous leaves (Eckstein et al. 1999). Typical symptoms of nutrient deficiency in conifer needles are reported in Table 1. Solberg et al. (1998) investigated the effects of nitrogen, magnesium, or potassium deficiency on concentrations of pigments in Norway spruce needles. Trees suffering from mineral deficiency were yellowish, experiencing up to a 50% reduction in pigment concentration. Compared to green trees, they also had a lower chlorophyll–carotenoid ratio. The ratio, however, seems to be unaffected by a deficiency in potassium. An interesting relationship was found between the concentration of α-carotene and nitrogen-deficient trees. It suggests that α-carotene can be considered the most sensitive pigment to any type of stress. The loss in pigment concentration is interpreted as an adaptive response in avoiding damages from excessive absorption of energy. This is because a loss in pigments is strictly correlated to a loss in photosynthetic units. In fact, the light-use efficiency of remaining pigmentation was found unchanged.

Determination of nitrogen and other nutrients is possible with remote sensing. Kokaly and Clark (1999), Kokaly (2001), and Kokaly et al. (2003) produced an interesting series of studies. They clearly demonstrated effectiveness of use of spectra derivatives and continuum-removal techniques as a way to improve spectral-features discrimination on a wide range of vegetation spectra. Both field and AVIRIS datasets were used in these studies.

The ability of EO-1Hyperion to detect nitrogen concentration in conifer and mixed deciduous forest canopies has been demonstrated by Smith et al. (2003). The authors, to determine nitrogen, chlorophyll, and other protein absorption features through imaging spectrometry, used EO-1Hyperion and AVIRIS datasets. Partial least square regression and spectra derivatives were found effective to relate canopy chemistry to sensor responses. Several nitrogen-absorbing features were detected at very similar wavelengths in AVIRIS and EO-1 Hyperion, and estimates from both sensors were considered satisfactory for forest monitoring.

Table 1. Symptoms of Mineral Nutrient Deficiency in Conifer Needles (adapted from Larcher 2003)

Deficient element	Function in plant	Symptoms of deficiency in needles of conifers
N nitrogen	Essential component of protoplasm and enzymes	Chlorophyll deficiency, discoloration, reduced growth, loss of needles
P phosphorous	Basal metabolism and syntheses (phosphorylation)	Reddening of needles, necrosis without previous chlorosis
S sulphur	Component of protoplasm and enzymes	Chlorosis of young needles
K potassium	Regulation of hydration, electrochemical effects, enzyme activation	Dry out of needle tips, shedding of needles
Ca calcium	Regulation of hydration, enzyme activator, signaling substance, control of elongation growth	Chlorosis of the tips of fir trees, followed by browning of needles
Mg magnesium	Regulation of hydration, basal metabolism	Chlorosis, mainly of older needles. Discoloration of needle tips in firs
Fe iron	Basal metabolism, nitrogen-metabolism, synthesis	Young needles yellow to white, older needles green
Mn manganese	Basal metabolism, nucleic-acid synthesis, chloroplast structure stabilizer	Young needles chlorotic
Zn zinc	Chlorophyll formation, enzyme activator, basal metabolism, biosynthesis of growth regulators	Young needles first chlorotic, then necrotic
Cu copper	Basal metabolism, nitrogen-metabolism, secondary metabolism	Chlorosis of young needles
B boron	Carbohydrate transport and metabolism, phenol metabolism, activation of growth regulators	

Conclusions

Many aspects of the selection and colonization processes of trees by bark beetle species need further detailed investigation. The exact cause and time of death of an attacked tree are not fully understood. Various species of fungi introduced in the host by the beetles have the ability to spread not only in the phloem, but also in the xylem. Some experimental studies on trees artificially inoculated with fungi associated with bark beetles have tried to determine the rate of spread of fungi into sapwood, and to establish the severity of damage suffered by the vascular system of the tree. This is critical, because it has been suggested that water and mineral uptake by the tree will be progressively impaired and the tree will suffer severe water stress. Both hydraulic and chemical signals related to the stress will trigger a tree defense response. Many details of the chain of events representing the response of the tree to beetle–fungus stress are still unknown. Some conifer species are able to store water in their sapwood to be used by the tree to cope with extended period of drought. In addition, conifer needles have developed anatomical structures to minimize water loss, protect the photosynthetic system from absorption of excess energy, and deal with freezing temperatures: the onset of visible water-stress symptoms in tree foliage could be retarded for many weeks or even months. This has important implications for remotely sensed detection of trees in green attack. It is possible that for the entire length of the green attack stage, changes in foliar optical properties do not exceed the natural range of variation of healthy vegetation.

Many studies have demonstrated the capability of remote sensing to retrieve vegetation water content and canopy biochemistry. Methods to improve the accuracy of the information extracted from the imagery are in development.

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